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THE PLIOCENE AND QUATERNARY FLAMINGOES OF AUSTRALIA

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ABSTRACT

From the Quaternary deposits of northeastern South Australia, material of what appears to be four species of flamingo has been recovered. These in order of size are referred to: *Xenorhynchopsis tibialis* de Vis, 1905, larger than extant species of flamingo; *Phoenicopterus ruber* Linnaeus, 1758, similar in size to modern *P. ruber; Xenorhynchopsis minor* de Vis, 1905, similar in size to *Phoeniconaias minor* (Linnaeus, 1758); and *Ocyplanus proeses* de Vis, 1905 including *Ibis* (?) *conditus* de Vis, 1905 and *Phoeniconaias gracilis* Miller, 1963, smaller than extant species of flamingo.

De Vis was unaware that some of the bones he named were those of flamingoes and assigned them as follows: *Xenorhynchopsis tibialis* and *X. minor* to the Ciconiidae, storks; *Ocyplanus proeses* to the Charadrii, waders; and *Ibis* (?) *conditus* to the Threskiornithidae, ibises. Miller was unaware that de Vis had named and incorrectly assigned some flamingo material. *Ocyplanus proeses* was reassigned by Lambrecht to the Laridae, gulls, and by Condon to the Rallidae, rails, both identifications which are also incorrect.

The material consists of bone fragments, most of which are not diagnostic at the generic level. Furthermore, the size of our samples of modern flamingoes is limited, and even though we have examined each species, a realistic grasp of variability within some species has not been reached in this study. We have, therefore, provisionally retained the generic and specific names that have priority as a convenience until more complete material allows a better evaluation of the systematic positions of the Pliocene and Quaternary flamingoes of Australia.

INTRODUCTION

Flamingoes are not part of the modern avifauna of Australia, and it was not until Miller (1963) described a series of bones from the late Cenozoic deposits of northeastern South Australia that their long history on this continent was recognised. Extinction of flamingoes in Australia has been a relatively recent event, probably occurring during the Late Pleistocene or even Holocene and appears tied to the disappearance of the relatively permanent shallow lakes, which characterized central Australia during much of the Cenozoic. According to Bowler (1982) loss of these lakes occurred in the last 400,000 years.

Since Miller (1963) demonstrated the presence of fossil flamingoes in Australia, further material has been found both in the field and in museum drawers, including some fossil Phoenicopteridae, that were collected by Gregory (1906) and described by de Vis (1905) as fossil species of stork, Ciconiidae, of ibis, Threskiornithidae, and of wader, Charadrii. Miller (1963) did not mention the fossil material of flamingoes that de Vis referred to other taxa, and was presumably unaware of de Vis' error. In fairness to de Vis and Miller, it should be realized that de Vis' reference collection did not contain any bones of flamingoes, so he assigned the unknown bones to the bird groups with the morphologies closest to what he had. Miller probably never examined the fossil flamingo material in the Queensland

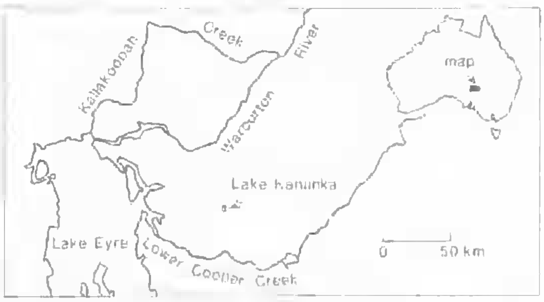

Fig. 1. Map of area where late Pliocene and Quaternary fossils of flamingoes were found in northeastern South Australia

TABLE 1. Elements and distributions of Quaternary flamingoes in northeastern South Australia.

Location	*X. tibialis*	*P. ruber*	*X. minor*	*O. proeses*	Phoenicopteridae
Kalakoopah Creek (Quaternary) Manku					stn UCMP 128455
Lake Kanunka (Pliocene)		tib UCMP 60562		tib UCMP 56887	
Site 1, V-5772		tmt UCMP 60583	hum UCMP 56882	tmt SAM P13650 UCMP 60561	
Lower Cooper Creek (Quaternary)					
Site 4, V-5380			tib UCMP 94688		
Site 8, V-5860	hum UCMP 56324				
Site 14, V-5866			hum UCMP 56360		
(age uncertain)					
Lower Cooper	tib QM F5515/6				
Unduwampa			tib QM F5517		
Wurdulumankula		tmt QM F5518		fem QM F5519	
Unknown sites (age uncertain)		fem QM F7013		tmt QM F5512	stn UCMP 69588

TABLE 2. Names, old and new, of specimens of Australian Quaternary flamingoes we have examined.

Specimen number	Element		New name this paper
		Old name from De Vis (1905)	
QM F5512	tmt	*Ocyplanus proeses* ht	same
F5515	tib	*Xenorhynchopsis tibialis* st	same lt
F5516	tib	*Xenorhynchopsis tibialis* st	same rf
F5517	tib	*Xenorhynchopsis minor* ht	same
F5518	tmt	*Xenorhynchopsis minor* rf	*Phoenicopterus ruber* rf
F5519	fem	*Ibis conditus* ht	*Ocyplanus proeses* rf
F7013	fem		*Phoenicopterus ruber* rf
		Old name from Miller (1963)	
SAM P13650	tmt	*Phoeniconaias gracilis* ht	*Ocyplanus proeses* rf
UCMP 56324	hum		*Xenorhynchopsis tibialis* rf
56360	hum	*Phoenicopterus ruber* rf	*Xenorhynchopsis minor* rf
56882	hum	*Phoeniconaias gracilis* rf	*Xenorhynchopsis minor* rf
56887	tib	*Phoeniconaias gracilis* rf	*Ocyplanus proeses* rf
60561	tmt	*Phoeniconaias gracilis* rf	*Ocyplanus proeses* rf
60562	tib		*Phoenicopterus ruber* rf
60583	tmt	*Phoenicopterus ruber* rf	same
69588	stn		Phoenicopteridae, indeterminate
94688	tib		*Xenorhynchopsis minor* rf
128455	stn		Phoenicopteridae, indeterminate

Museum collections. Because of this unavoidable oversight, some changes in nomenclature are now necessary.

This paper reviews the Quaternary and Pliocene material of flamingoes (Tables 1 and 2), including that described by de Vis (1905) and Miller (1963) from northeastern South Australia (see Fig. 1). In other papers we will review the earlier Tertiary material of flamingoes, which has a somewhat wider distribution in inland Australia.

ABBREVIATIONS

The following abbreviations have been used in this paper: AM, Australian Museum, Sydney; ANWC, Australian National Wildlife Collection, Division of Wildlife and Rangelands Research, CSIRO, Canberra; NMV, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; SAfM, South African Museum, Cape Town; UCMP, University of California, Museum of Paleontology, Berkeley; UCMVZ, University of California, Museum of Vertebrate Zoology, Berkeley; @ = approximately; fem = femur; hum = humerus; tib = tibiotarsus; tmt = tarsometatarsus; stn = sternum; ht = holotype; lt = lectotype; st = syntype; rf = referred.

COMPARATIVE MATERIAL

The main comparative material utilized in this study has been the extensive avian osteological collections in the Australian Museum, the Australian National Wildlife Collection, and the Museum of Victoria, which include representatives of almost all extant non-passeriform families and of the extinct Australian, American, and European Palaelodidae. Also available for comparison were all of the Tertiary flamingoes from Australia that were reported on by Miller (1963) and what has been found since, as well as casts of *Elornis anglicus* and *Leakeyornis aethiopicus*. The remaining comparisons were made with descriptions of all known fossil flamingoes.

The following modern flamingo material was available:

Phoenicopterus ruber: AM S424, S592, S594, S599, S600, S603, and O.56875; NMV B737, B738 ♀ and B748. SAM B5097 ♂, B11462, B11548 and B11552. The tarsometatarsi of these specimens, except for NMV B738, are all longer than 30 cm and, therefore, of males according to the tarsal measurements given in Brown *et al.* (1982), Blake (1977) and Cramp (1977).

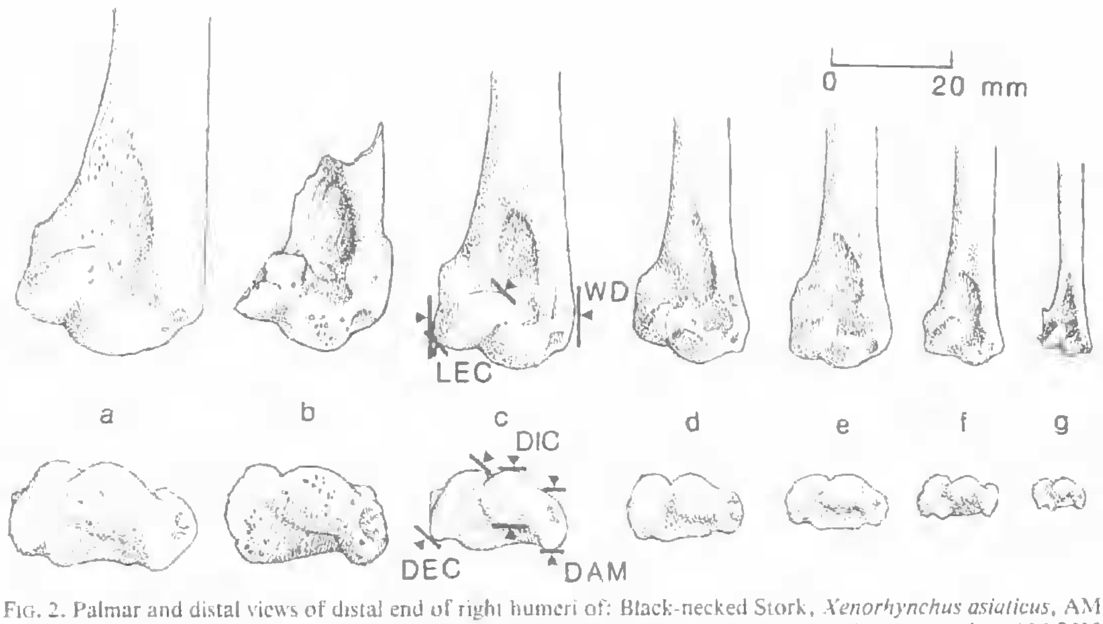

FIG. 2. Palmar and distal views of distal end of right humeri of: Black-necked Stork, *Xenorhynchus asiaticus*, AM B4139 (a); rf *Xenorhynchopsis tibialis*, UCMP 56324 (b); Greater Flamingo, *Phoenicopterus ruber*, AM S599 (c); Straw-necked Ibis, *Threskiornis spinicollis*, ANWC BS2986 (d); Lesser Flamingo, *Phoeniconaias minor*, ANWC BS2985 (e); Bush Stone-Curlew, *Burhinus magnirostris*, ANWC BS1855 (f); Banded Stilt, *Cladorhynchus leucocephalus*, SAM B31542 (g). Measurements for Tables 3, 4 and 11 are indicated as follows: WD = width of distal end, LEC = length of external condyle, DEC = depth of external condyle, DIC = depth of internal condyle and DAM = depth of attachment of *M. pronator brevis*.

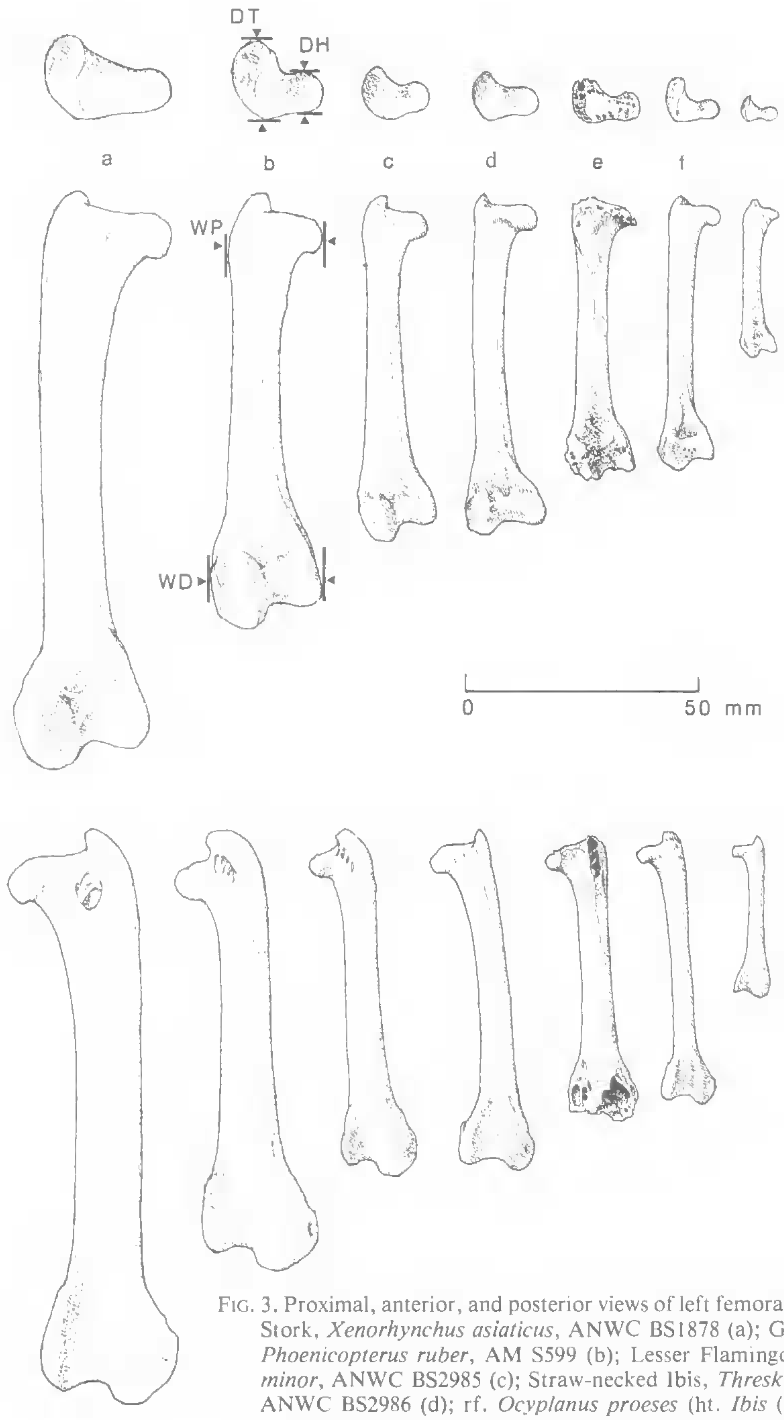

FIG. 3. Proximal, anterior, and posterior views of left femora of: Black-necked Stork, *Xenorhynchus asiaticus*, ANWC BS1878 (a); Greater Flamingo, *Phoenicopterus ruber*, AM S599 (b); Lesser Flamingo, *Phoeniconaias minor*, ANWC BS2985 (c); Straw-necked Ibis, *Threskiornis spinicollis*, ANWC BS2986 (d); rf. *Ocyplanus proeses* (ht. *Ibis* (?) *conditus*, QM F5519 (e); Bush Stone-Curlew, *Burhinus magnirostris*, ANWC BS1855 (f); Banded Stilt, *Cladorhynchus leucocephalus*, SAM B31542 (g). Measurements for Tables 5, 6 and 11 are indicated as follows: WP = width of proximal end, WD = width of distal end, DT = depth of trochanter and DH = depth of head.

Phoenicopterus ruber chilensis: AM S549; NMV B12740; SAM B25448 ♂; UCMVZ 125157 ♂, 12158 ♀, and 140923 ♂.

Phoeniconaias minor: ANWC BS2985 ♀; SAfM Zo57025 ♂; UCMVZ 133408 ♀, 133409 ♀, 133410 ♀ and 133411 ♂.

Phoenicoparrus andinus: UCMVZ 126566 ♀, 126567 ♂ and 129326 ♂.

Phoenicoparrus jamesi: UCMVZ 154304 ♂.

DIAGNOSIS OF ELEMENTS OF PHOENICOPTERIDAE REPRESENTED BY AUSTRALIAN PLEISTOCENE MATERIAL

The skeletal elements of Australian Pleistocene flamingoes that are available can be diagnosed from those of other avian families as follows:

STERNUM. Anterior end. In anterior view, ventral manubrial spine robust and triangular in shape with apex pointing ventrally; line dividing left from right coracoidal sulcus not perpendicular, but courses diagonally between sulci terminating on right side of base of ventral manubrial spine; coracoidal sulci with robust, but low and rounded dorsal lips; in ventral view, carina does not originate from base of manubrial spine.

HUMERUS. Distal end (Fig. 2). In palmar view, entepicondylar prominence low and gently rounded, not protruding far internally; where preserved, ectepicondylar prominence low, not protruding as a process; brachial depression elongate and deep; attachment for anterior articular ligament narrow and elongate, with long axis parallel to long axis of shaft; ectepicondyle subdued, not extending laterally beyond external condyle; in medial view, distal end of bone shallow, not inflated.

FEMUR. (Fig. 3) Proximal end. In proximal view, head large, with depth being somewhat greater than one-half that of trochanter; anterior border of proximal end deeply concave, and highly curved, not straight; posterior border does not protrude far posteriorly; head does not protrude far internally beyond shaft, thus having very short neck; trochanter arises abruptly from nearby flat proximal articular surface, and forms tall crest that is concave internally.

Distal end. In posterior view, popliteal area broad, shallow, almost flat and marked with prominent ligamental scar in the middle; medial margin of popliteal area very straight, elongate ridge that merges with posterior intermuscular line

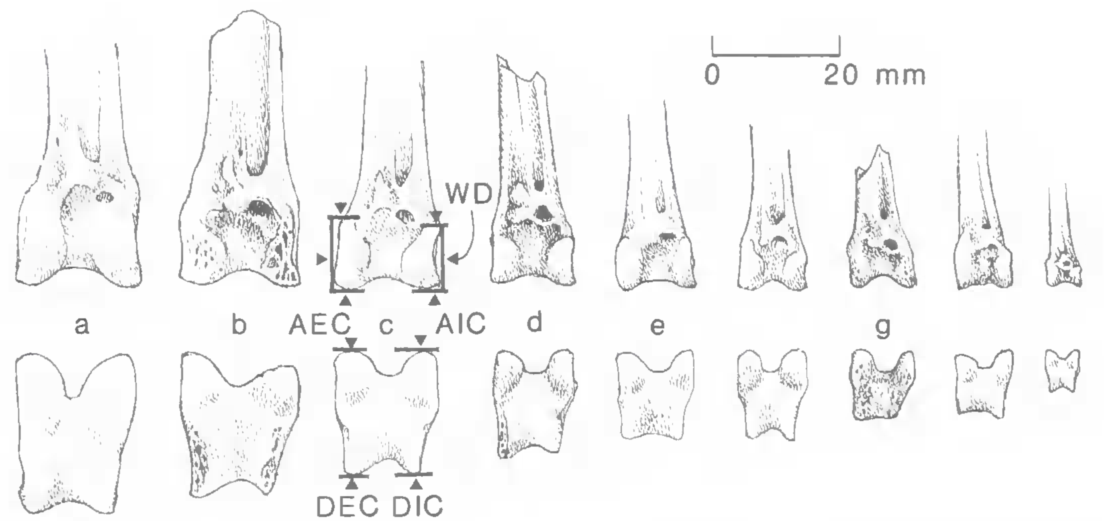

FIG. 4. Anterior and distal views of distal end of right tibiotarsi of: Black-necked Stork, *Xenorhynchus asiaticus*, ANWC BS1878 (a); lt. *Xenorhynchopsis tibialis* QM F5515 (b); Greater Flamingo, *Phoenicopterus ruber*, AM S599 (c); ht. *Xenorhynchopsis minor*, QM F5517 (d); Straw-necked Ibis, *Threskiornis spinicollis*, ANWC BS2986 (e); Lesser Flamingo, *Phoeniconaias minor*, ANWC BS2985 (f); rf. *Ocyplanus proeses*, UCMP 56887 (g); Bush Stone-Curlew, *Burhinus magnirostris*, ANWC BS1855 (h); Banded Stilt, *Cladorhynchus leucocephalus*, SAM B31542 (i). Measurements for Tables 7, 8, 11 and 12 and Figure 6 are indicated as follows: WD = width of distal end, DIC = depth of internal condyle, DEC = depth of external condyle, AIC = anterior length of internal condyle and AEC = anterior length of external condyle.

proximally and which lacks any protuberances along it; internal condyle anteroposteriorly compressed, with internal surface of shaft flattened and smooth.

TIBIOTARSUS. Distal end (Fig. 4). In anterior view, distal end mediolaterally compressed, and condyles not elongate proximodistally; tendinal groove offset toward medial side of bone, not centred on shaft; tendinal bridge not 'broad' proximodistally; marked ligamental protuberance present on laterodistal end of supratendinal bridge that merges with short ridge, which itself lies well internal to lateral border of shaft; condylar fossa deeply excavated, even undercutting bases of condyles; internal condyle in most cases extends only slightly distal to external condyle; in distal view, condyles deep and width across them decidedly greater anteriorly than posteriorly; posterior articular surface distinct from anterior; condyles not of subequal depth.

TARSOMETATARSUS. Distal end (Fig. 5). Trochlea IV extends decidedly farther distally than II, and III extends farthest; in medial view, distal end of trochlea II flattened or only slightly curved, not highly convex; in distal view, trochleae highly arched, resulting from trochlea II being twisted posteriorly and externally from the front of the tarsometatarsus; trochlea III narrow and deep, not shallow and broad; anterior border of trochlea II broader than posterior border.

SYSTEMATIC POSITIONS OF AUSTRALIAN PLIOCENE AND QUATERNARY MATERIAL

The fossil material of Phoenicopteridae from the Pliocene and Quaternary of Australia which we have examined includes that reported on by de Vis (1905) and Miller (1963) and is summarised in Tables 1 and 2. As suggested in Rich and van Tets (1982), this material appears to include four size categories (Tables 3-10, Figs 6 & 7): larger than the Greater Flamingo, *Phoenicopterus ruber*; similar in size in *P. ruber*; similar in size to the Lesser Flamingo, *Phoeniconaias minor*; and smaller than *P. minor*.

The fossil material is still too rare and fragmentary for us to decide whether these forms

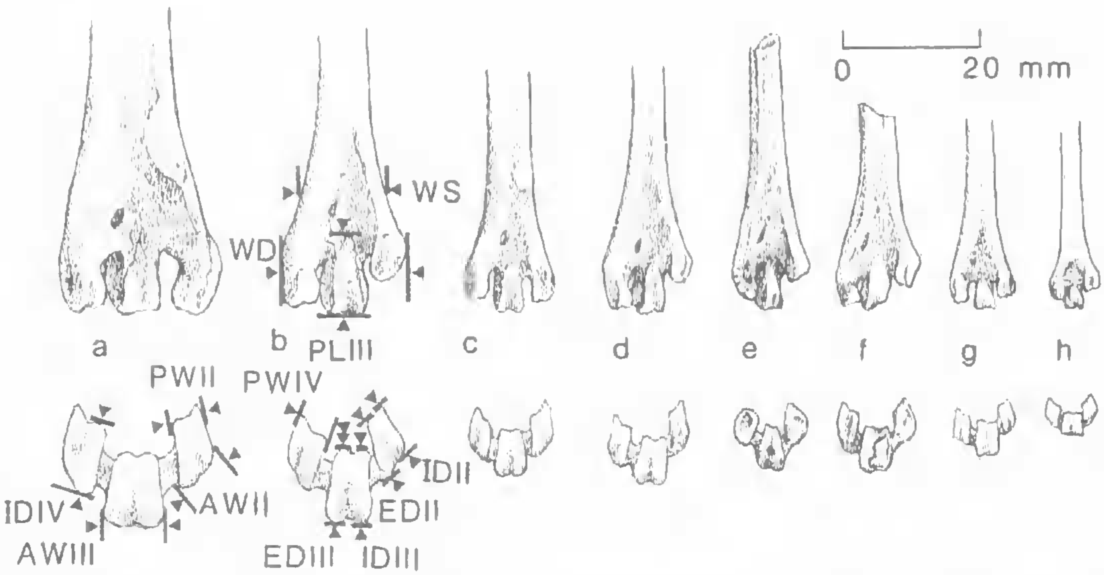

FIG. 5. Posterior and distal views of distal end of left tarsometatarsi of: Black-necked Stork, *Xenorhynchus asiaticus* ANWC BS1878 (a); Greater Flamingo, *Phoenicopterus ruber* AM S599 (b); Straw-necked Ibis, *Threskiornis spinicollis*, ANWC BS2986 (c); Lesser Flamingo, *Phoeniconaias minor* ANWC BS2985 (d); ht. *Ocyplanus proeses* QM F5512 (e); cf. *Ocyplanus proeses* (ht. *Phoeniconaias gracilis*) SAM P13650 (f); Bush Stone-Curlew, *Burhinus magnirostris*, ANWC BS1855 (g); Banded Stilt, *Cladorhynchus leucocephalus*, SAM B31542 (h). Measurements for Tables 9, 10, 11 and 12 and Figure 7 are indicated as follows: WS = width of shaft at proximal end of distal foramen, WD = width of distal end, IDII = internal depth of trochlea II, EDII = external depth of trochlea II, AWII = anterior width of trochlea II, PWII = posterior width of trochlea, II, IDIII = internal depth of trochlea III, EDIII = external depth of trochlea III, AWIII = anterior width of trochlea III, PLIII = posterior length of trochlea III, IDIV = internal depth of trochlea IV, PWIV = posterior width of trochlea IV.

are congeneric or not with extant genera, and indeed where species boundaries should be drawn. Differences can be observed, but how much this is related to variability within a taxon and how much a reflection of real taxonomic difference is not yet clear. We, therefore, for convenience, have retained the following names for four size categories: *Xenorhynchopsis tibialis* de Vis, 1905; *Phoenicopterus ruber* Linnaeus, 1758; *Xenorhynchopsis minor* de Vis, 1905; and *Ocyplanus proeses* de Vis, 1905. Only when larger samples are known will an assessment approaching that of modern species be possible.

Xenorhynchopsis tibialis

Citation: de Vis, 1905. *Ann. Qd Mus.* 6: 9-10, pl. 1., fig. 6.

SYNTYPES: QM F5515 and F5516, distal ends of a right and a left tibiotarsus, Lower Cooper Creek, South Australia, Quaternary.

De Vis described QM F5515 and F5516 as syntypes of a new genus and species of stork, Ciconiidae. They are similar in size to the tibiotarsi of the Black-necked Stork or Australian Jabiru, *Ephippiorhynchus* (*Xenorhynchus*) *asiaticus*, with which he compared it. QM F5515 and F5516 resemble the tibiotarsi of Phoenicopteridae and differ from those of Ciconiidae, in distal view, by being decidely broader anteriorly than they are posteriorly, by having a very prominant ligamental attachment at the base of the supratendinal bridge, and a very deeply excavated anterior surface between the two condyles. QM F5515 and F5516 differ from the tibiotarsi of other Phoenicopteridae by being larger than those of the largest extant species *Phoenicopterus ruber* (Table 5); and in that the internal condyle projects decidedly farther distally than the external (Fig. 4).

Qualitative characters that may distinguish *Xenorhynchopsis* from other genera are rather questionable: in *X. tibialis* the distal end appears deeper relative to width; the shaft flares less at the distal end; the ligamental groove on the lateral side of the shaft is located relatively nearer the anterior border. It appears to differ from *Leakeyornis* in that the ligamental prominence on the distal end

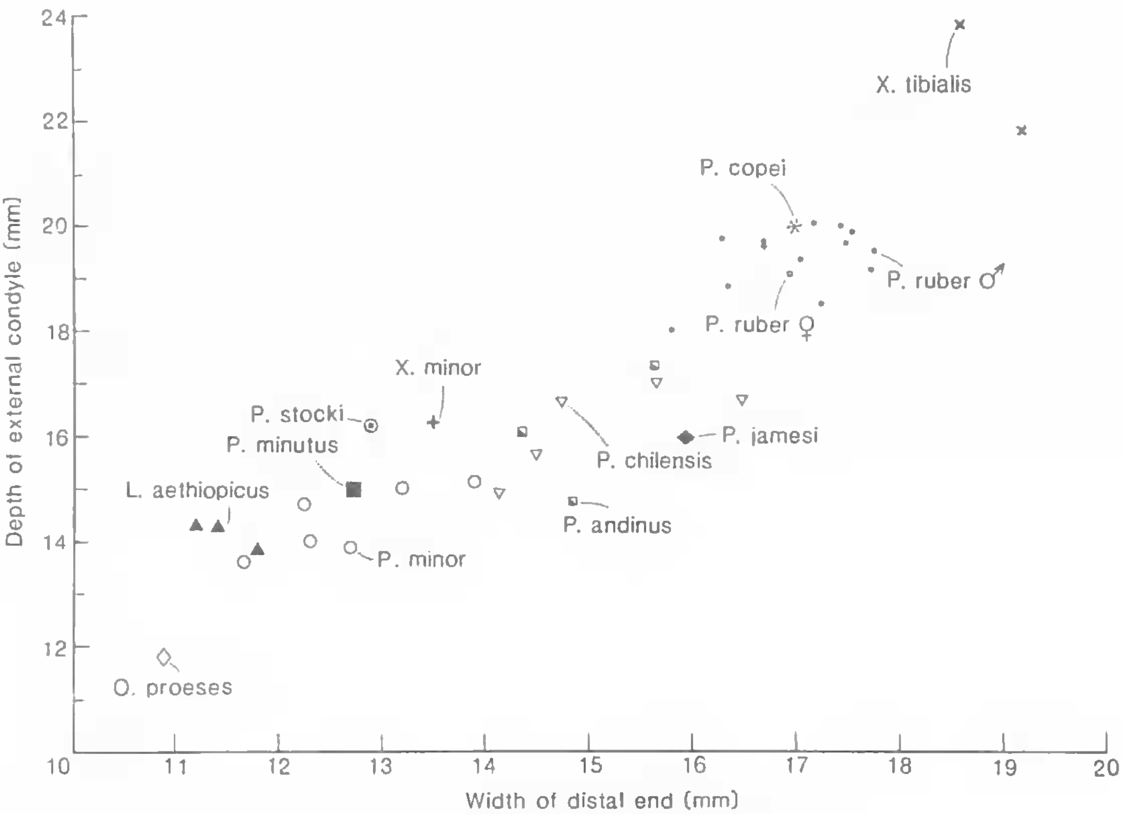

FIG. 6. Comparison of distal tibiotarsal measurements of extant and extinct species of flamingo.

of the supratendinal bridge is not subdued, and the supratendinal canal is broader. Direct comparison with *Phoeniconotius* is not possible, as that genus is known only from a tarsometatarsus and phalanges.

We hereby designate QM F5515 as the lectotype of *Xenorhynchopsis tibialis* and refer QM F5516 to *X. tibialis*.

ADDITIONAL REFERRED MATERIAL

Humerus: UCMP 56324, left distal fragment, Cooper Creek, site 8, UCMP V-5860, South Australia, Malkuni Fauna, Katipiri Sands; collected as float from a river channel in the western fork of Cooper Creek about one-half mile south of Kittipirra, Quaternary.

In shape, this humerus differs from that of the extant genera of flamingoes in having a relatively deeper brachial depression; a relatively shorter ventral supracondylar tubercle that is concave palmarly, not flat; and perhaps a more inflated distal end. More complete material is needed to accurately estimate the degree of inflation, however. The humerus differs from that of *Leakeyornis* in that the internal condyle does not extend further distally relative to the external condyle than in modern genera; the condyles appear to be relatively more inflated, and the distal end is deeper relative to its width (Tables 3, 4 & 11).

Phoenicopterus ruber

Citation: Linnaeus, 1758. *Syst. Nat.* ed. 10, 1: 139.

REFERRED MATERIAL

Tarsometatarsus: QM F5518, right distal fragment, Wurdulumankula, South Australia, age uncertain.

De Vis (1905) referred this tarsometatarsus to *Xenorhynchopsis minor*, as a species of stork smaller than his *X. tibialis*. QM F5518 is similar in shape to the tarsometatarsi of Phoenicopteridae in the position of the trochlea for digit II being more ventral than in Ciconiidae. QM F5518 is decidedly more mediolaterally compressed than in *Phoenicoparrus*, and thus more like this element in *Phoeniconais* and *Phoenicopterus*. QM F5518 is similar in size and shape to small tarsometatarsi of *P. ruber*; it does appear to differ slightly from our sample of *P. ruber*, however, in having a

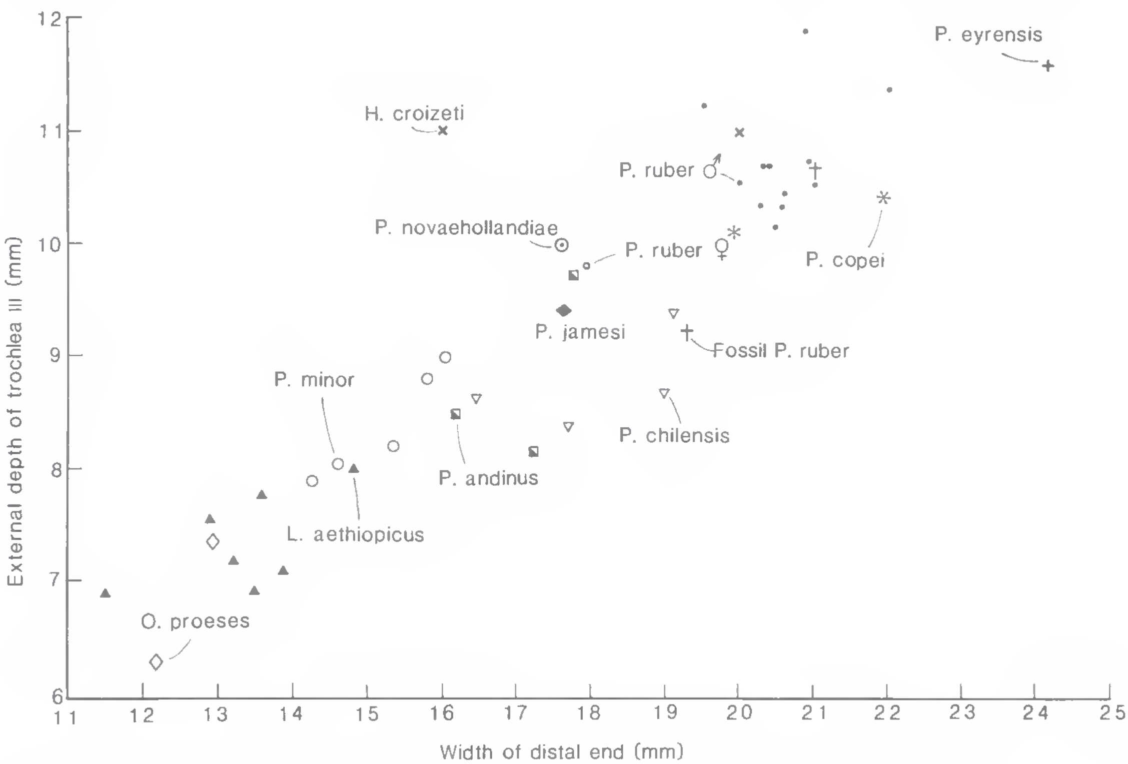

FIG. 7. Comparison of distal tarsometatarsal measurements of extant and extinct species of flamingo.

relatively shallower trochlea IV, although there is definitely some wear on the bone that might have overemphasized this. *P. copei* is similar in size to *P. ruber* (Tables 8, 10 and 12), but according to Shufeldt (1892) has longer wings, legs and toes, and a coracoid with a narrower dorsal end. These are characters that are not available for comparison in the Pliocene and Quaternary material of Australian flamingoes. For the present, because of its size we provisionally refer QM F5518 to *P. ruber*.

Femur: QMF 7013 left, proximal fragment, probably from northeastern South Australia.

This femur was found in the de Vis collection in the Queensland Museum with no information as to its origin. It is not one of the few missing specimens that were described by de Vis. Its preservation is compatible with that of fossil material from northeastern South Australia.

In shape and size, QMF 7013 is similar to the femur of a large *Phoenicopterus ruber*, to which species we tentatively refer it. It differs from *Leakeyornis* in having a flat anterior shaft surface near the proximal end and a posterior expansion of the trochanter.

Tibiotarsus: UCMP 60562, left distal fragment, Stirton Quarry, Lake Kanunka, Site 1, UCMP V-5772, South Australia, Tirari Formation, Pliocene. This tibiotarsus was found at the base of an escarpment on the northeast side of the northern part of the bluffs immediately to the west of Lake Kanunka. It differs slightly in shape from that of *P. ruber* in that the tendinal canal is decidedly deeper and broader, and the tendinal

TABLE 3. Measurements in mm of the humeri of Australian Quaternary flamingoes.

	X. tibialis	*X. minor*	
	UCMP 56324 rf	UCMP 56360 rf	UCMP 56882 rf
Width of distal end		@22	@19
Length of external condyle	15.2	11.6	9.8
Depth of external condyle	15.8	11.8	10.5
Depth of internal condyle	9.1		5.9
Depth at attachment of *M. pronator brevis*	12.7	>8.6	7.8

TABLE 4. Measurements in mm of the humeri of modern flamingoes.

		P. ruber ♂	*P. ruber* ♀	*P. chilensis*	*P. andinus*	*P. minor*
Width of distal end	$\bar{x}$	25	23	23.5	22	19
	range	23–26	—	23–24	—	18–21
	n	13	1	3	1	3
	sd	0.8	—	0.5	—	1.4
Length of external condyle	$\bar{x}$	14	12	14	11	10
	range	12–15	—	14–15	—	9–11
	n	13	1	3	1	3
	sd	1.0	—	0.3	—	0.5
Depth of external condyle	$\bar{x}$	15	13	14	13	11
	range	13–16	—	12–15	—	10–12
	n	13	1	3	1	3
	sd	0.7	—	1.0	—	0.8
Depth of internal condyle	$\bar{x}$	9	9	9	8	7
	range	8–10	—	9–10	—	6–8
	n	13	1	3	1	3
	sd	0.7	—	0.3	—	0.7
Depth at attachment of *M. pronator brevis*	$\bar{x}$	10	10	9	—	8
	range	9–11	—	9–9	—	—
	n	11	1	3	—	1
	sd	0.5	—	0.2	—	—

TABLE 5. Measurements in mm of the femora of Australian Quaternary flamingoes.

	P. ruber	*O. proeses*
	QM F7013 rf	QM F5519 rf
Width of proximal end	>18.6	@13.6
Width of distal end	—	@15.1
Depth of trochanter	—	>9.1
Depth of head	@10.1	@6.2

groove on the lateral side of the external condyle is displaced farther anteriorly than in any of the modern genera. It differs from the tibiotarsus of *Leakeyornis* in having a very prominent ligamental attachment on the distal end of the tendinal bridge and in having a deeply incised tendinal canal. In size, UCMP 60562 agrees with *Phoenicopterus ruber*, to which we provisionally refer it.

Tarsometatarsus: UCMP 60583, right distal fragment, Lake Kanunka, Site 1, UCMP V-5772, South Australia, Tirari Formation, Pliocene.

TABLE 6. Measurements in mm of the femora of modern flamingoes.

		P. ruber ♂	*P. ruber* ♀	*P. chilensis*	*P. andinus*	*P. minor*
Width of proximal end	$\bar{x}$	23	21	20	20	17
	range	20–24	—	18–22	19–20	15–18
	n	13	1	6	3	5
	sd	1.0	—	1.2	0.7	1.0
Width of distal end	$\bar{x}$	26	24	23	22	18
	range	24–27	—	23–24	—	17–20
	n	13	1	3	1	3
	sd	0.8	—	0.4	—	1.3
Depth of trochanter	$\bar{x}$	18	17	17	15	13
	range	17–20	—	16–17	—	12–14
	n	13	1	3	1	3
	sd	0.9	—	0.5	—	0.5
Depth of head	$\bar{x}$	10	9	10	9	7
	range	9–11	—	8–10	8–10	6–8
	n	13	1	6	3	5
	sd	0.4	—	0.7	0.6	0.5

TABLE 7. Measurements in mm of the tibiotarsi of Australian Quaternary flamingoes.

	X. tibialis		*P. ruber*	*X. minor*		*O. proeses*
	QM F5515 lt	QM F5516 rf	UCMP 60562 rf	QM F5517 ht	UCMP 94688 rf	UCMP 56887 rf
Width of distal end	@19.2	18.6		13.5	>14.9	10.9
Depth of internal condyle		>22.3	19.3	15.9		
Depth of external condyle	21.8	>23.8		16.3		>11.8
Anterior length of internal condyle			8.8	6.9	@7.7	5.8
Anterior length of external condyle	11.5	@9.2		9.0		6.5

Miller (1963) described and figured this tarsometatarsus, similar in size and shape to a large tarsometatarsus of *Phoenicopterus ruber*, to which species he referred it. We tentatively agree with this referral.

Xenorhynchopsis minor

Citation: de Vis, 1905. *Ann. Qd Mus.* **6**: 10, pl. I, II, fig. 1.

HOLOTYPE: QM F5517, distal end of a right tibiotarsus, Unduwampa, South Australia, Quaternary.

De Vis described QM F5517 as the holotype of a small species of stork in his genus *Xenorhynchopsis*. In size and shape the holotype is similar to *Phoeniconaias minor*, except that the shaft is somewhat stouter in *Xenorhynchopsis minor*. In *X. minor* the external condyle is deeper relative to distal end width, the internal condyle is relatively shorter, and there is a greater difference in the lengths of the internal and external condyles when they are viewed anteriorly than in *P. minor*. The tibiotarsus of *X. minor* is larger than that in *Leakeyornis aethiopicus* (Tables 7 & 11), and it differs in having a very large distal opening of the tendinal canal, but it is very similar in all other characters. Like in *Xenorhynchopsis tibialis*, the condyles of *X. minor* are deeper relative to width, and thus *Xenorhynchopsis* differs from the living genera and *Leakeyornis*. Both *X. tibialis* and *X. minor* flare only slightly distally, apparently not as much as in the living genera, and both have very large distal openings of the tendinal canal; neither have a deeply notched distal border of the internal condyle, thus differing from the species in modern genera. *Phoenicopterus stocki* (Miller 1944) from the Pliocene of North America and *P. minutus* (Howard 1955) from the Pleistocene of North America are both about the same size as *X. minor*

TABLE 8. Measurements in mm of the tibiotarsi of modern flamingoes.

		P. ruber ♂	*P. ruber* ♀	*P. chilensis*	*P. andinus*	*P. jamesi*	*P. minor*
Width of distal end	x̄	17	16	15	15	16	13
	range	16–18	—	14–17	14–16	—	12–14
	n	13	1	6	3	1	6
	sd	0.6	—	1.0	0.7	—	0.8
Depth of internal condyle	x̄	20	18	16	16	16.5	15
	range	19–20	—	15–17	15–18	—	14–15
	n	13	1	6	3	1	6
	sd	0.6	—	0.6	1.1	—	0.5
Depth of external condyle	x̄	19	18	16	16	16	14
	range	19–20	—	15–17	15–17	—	13–15
	n	13	1	6	3	1	6
	sd	0.6	—	0.8	1.2	—	0.6
Anterior length of internal condyle	x̄	10	9	8	8	7.5	7
	range	9–11	—	8–9	—	—	6–8
	n	13	1	3	1	1	4
	n	13	1	6	3	1	6
	sd	0.6	—	0.6	1.1	—	0.5
Depth of external condyle	x̄	19	18	16	16	16	14
	range	19–20	—	15–17	15–17	—	13–15
	n	13	1	6	3	1	6
	sd	0.6	—	0.8	1.2	—	0.6
Anterior length of internal condyle	x̄	10	9	8	8	7.5	7
	range	9–11	—	8–9	—	—	6–8
	n	13	1	3	1	1	4
	sd	0.5	—	0.6	—	—	0.4
Anterior length of external condyle	x̄	11	10	9	9	9	8
	range	10–12	—	8–9	—	—	8–9
	n	13	1	4	1	1	4
	sd	0.5	—	0.3	—	—	0.4

(Tables 7, 8 & 12), and both appear also to have deep condyles, with *P. stocki* being deepest (Howard 1955). *P. minutus* has a relatively shorter internal condyle, evidently a relatively higher intercondylar tubercle (Howard 1955), a notch on the distal border of the internal condyle that is well behind the centre of the condyle, not near its centre, and the shaft flares more broadly at the distal end. *X. minor* appears to differ from both *P. stocki* and *P. minutus* in having a relatively broad intercondylar notch, as in living flamingoes, rather than a narrow one.

REFERRED MATERIAL

Tibiotarsus: UCMP 94688, left distal fragment, Cooper Creek, Site 4, UCMP V-5380, South Australia, Malkuni Fauna, Katipiri Sands, Quaternary. Collected from a sandbar in the main channel of Cooper Creek.

This tibiotarsus is similar in size to those of

TABLE 9. Measurements in mm of the tarsometatarsi of Australian Quaternary flamingoes.

	P. ruber		*O. proeses*		
	QM F5518 rf	UCMP 60583 rf	QM F5512 hi	SAM P13650 rf	UCMP 60561 rf
Width of shaft at proximal end of distal foramen	14.2		8.6	9.8	
Width of distal end	@19.2	>21.0	12.2	13.0	
Internal depth of trochlea II				6.1	
External depth of trochlea II	7.4	>8.1	5.1	6.0	5.8
Anterior width of trochlea II	>6.4	9.1	@4.2	4.7	5.2
Posterior width of trochlea II	>4.8			3.1	
Internal depth of trochlea II	8.9	10.6	6.1		6.9
Anterior width of trochlea II	>6.4	9.1	@4.2	4.7	5.2
Posterior width of trochlea II	>4.8			3.1	
Internal depth of trochlea III	8.9	10.6	6.1		6.9
External depth of trochlea III	9.2	10.7	6.3	7.4	>7.2
Anterior width of trochlea III	>7.4	>7.9	>4.8	>5.1	>5.4
Posterior length of trochlea III	@10.6	10.9	9.0	>8.1	
Internal depth of trochlea IV	>7.7			6.2	
Posterior width of trochlea IV	5.8			3.2	

TABLE 10. Measurements in mm of the tarsometatarsi of modern flamingoes.

		P. ruber ♂	*P. ruber* ♀	*P. chilensis*	*P. andinus*	*P. jamesi*	*P. minor*
Width of shaft at proximal end of distal foramen	$\bar{x}$	15	13	15	11	14	12
	range	14–17	—	14–15	—	—	11–13
	n	12	1	3	1	1	3
	sd	0.8	—	0.1	—	—	0.7
Width of distal end	$\bar{x}$	21	18	18	17	18	15
	range	19–22	—	16–20	16–18	—	14–16
	n	12	1	6	3	1	5
	sd	0.6	—	1.1	0.8	—	0.8
Internal depth of trochlea II	$\bar{x}$	8	7	7	—	—	7
	range	7–10	—	7–8	—	—	—
	n	12	1	5	—	—	1
	sd	0.5	—	0.4	—	—	—
External depth of trochlea II	$\bar{x}$	9	7.5	8	7	7	6
	range	8–10	—	7–9	6–8	—	6–8
	n	12	1	5	3	1	6
	sd	0.8	—	0.6	0.9	—	0.5
Anterior width of trochlea II	$\bar{x}$	7	7	6	7	7	5
	range	6–8	—	4–7	—	—	4–6
	n	12	1	6	1	1	4
	sd	0.4	—	0.9	—	—	0.8
Posterior width of trochlea II	$\bar{x}$	5	—	5	5	5	4
	range	5–6	—	4–5	4–5	—	3–5
	n	12	—	4	3	1	5
	sd	0.3	—	0.3	0.3	—	0.4
Internal depth of trochlea III	$\bar{x}$	11	10	9	9	9	8
	range	10–11	—	8–10	8–11	—	8–9
	n	11	1	5	3	1	5
	sd	0.5	—	0.4	1.3	—	0.4
External depth of trochlea III	$\bar{x}$	11	10	9	9	9	8
	range	10–12	—	8–10	8–10	—	8–10
	n	12	1	5	3	1	5
	sd	0.5	—	0.5	0.8	—	0.5
Anterior width of trochlea III	$\bar{x}$	8	8	7	7	7	6
	range	8–9	—	5–8	—	—	6–7
	n	12	1	5	1	1	3
	sd	0.4	—	1.2	—	—	0.5
Posterior length of trochlea III	$\bar{x}$	12	10	10	10	11	9
	range	11–13	—	9–11	—	—	9–10
	n	12	1	3	1	1	3
	sd	0.5	—	1.1	—	—	0.9
Internal depth of trochlea IV	$\bar{x}$	10	9.5	8	8	8	7
	range	9–11	—	8–9	7–8	—	7–8
	n	12	1	5	3	1	5
	sd	0.5	—	0.3	0.6	—	0.3
Posterior width of trochlea IV	$\bar{x}$	6	5	5	5	5	4
	range	5–7	—	5–6	4–5	—	4–4
	n	12	1	4	3	1	6
	sd	0.3	—	0.4	0.3	—	0.1

Phoenicopterus minor. It is very heavily weathered, and we only tentatively refer it to *Xenorhynchopsis minor* on the basis of size.

Humerus: UCMP 56360, left distal fragment, Cooper Creek, site 14, UCMP V-5866, South Australia, Malkuni Fauna, Katipiri Sands. Collected from the northern side of the channel at a prominent west bend, where bones were found in place or as float derived from a sand-filled channel cut into red-green mottled arenaceous clays and overlain disconformably by a grey-brown argillaceous sandstone and dune sands.

On UCMP 56360 and the humeri of *Phoenicopterus* the dorsal supracondylar process is not as prominent as it is in *Phoeniconaias* and *Phoenicoparrus*. UCMP 56360 differs from the

TABLE 11. Measurements in mm of the humeri, femora, tibiotarsi and tarsometatarsi of Tertiary flamingoes of the World from Rich and Walker (1983).

	L. aethiopicus		*H. croizeti*		*P. eyrensis*	*P. novaehollandiae*	*P. floridanus*
	range	n	range	n	n = 1	n = 1	n = 1
HUMERUS							
Width of distal end	16–18	7					
Length of external condyle	9–10.5	8					
Depth of external condyle	9–10.5	8					
FEMUR							
Width of distal end	15–18.5	3					
TIBIOTARSUS							
Width of distal end	11–12	3	15.9	1			16.5
Depth of internal condyle	12–14	3	11.5	1			
Depth of external condyle	@14	3	18.5	1			
Anterior length of internal condyle	6–7	2	8.5	1			
Anterior length of external condyle	7–8	2	10.1	1			
TARSOMETATARSUS							
Width of distal end	11–15	7	16–20	2	@24.4	17.6	
External depth of trochlea II	5–7	6			9.2	8.4	
Anterior width of trochlea II	4.5–5	4	4.5	1	8.7	6.6	
Internal depth of trochlea III	7–8	5	10.5	1	11.2	9.8	
External depth of trochlea III	7–9	9	11.0	1	11.6	10.0	
Anterior width of trochlea III	5–6	4	7–9	2	11.5	7.8	
Posterior length of trochlea III	7–9	7			10.9	@10	
Internal depth of trochlea IV	6–7	9				9.7	
Posterior width of trochlea IV	3.5–5	7	6.0	1		5.6	

humerus of *Leakeyornis* in having: only a small area of the brachial depression that is deep; the internal condyle not extending much beyond the external condyle; and the condyles inflated as in living flamingoes. Miller (1963) referred UCMP 56360 to *Phoenicopterus ruber*, because it is similar in size and shape to the humerus of UCMVZ 140923, labelled as a male of *Phoenicopterus ruber ruber*. The tarsometatarsal length of UCMVZ 140923 is 253 mm, which is within the range for males of *Phoenicopterus ruber chilensis*, and of females of *P. r. ruber* and *P. r. roseus*, but is too small for males of *P. r. ruber* and *P. r. roseus* as indicated in Blake (1977) and Cramp (1977). Our other measurements also suggest that UCMVZ 140923 has been mislabelled and misidentified and should be referred to *P. chilensis* rather than to *P. ruber*. We tentatively refer UCMP 56360 to *Xenorhyncopsis minor*, in part because it is slightly smaller than our sample of *P. chilensis* (including UCMVZ 140923), substantially smaller than our sample of *P. ruber*, and slightly larger than our sample of *Phoeniconaias minor*.

Humerus: UCMP 56882, left distal fragment, Lake Kanunka, Site 1, UCMP V-5772, South Australia, Tirari Formation, Pliocene.

Miller (1963) referred this humerus to *Phoeniconaias gracilis*, but noted that in size it was similar to *Phoeniconaias minor*. Mainly because of its size we tentatively refer it to *Xenorhynchopsis minor*.

Ocyplanus proeses

Citation: de Vis, 1905. *Ann. Qd Mus.* 6: 8-9, pl. I, fig. 5b.

New Synonymy:

Ibis (?) *conditus* de Vis, 1905. *Ann. Qd Mus.* 6: 10-11, pl. II, fig. 2.

Phoeniconaias gracilis Miller, 1963. *Condor* 65: 294-6, fig. 4.

HOLOTYPE OF *OCYPLANUS PROESES*

Tarsometatarsus: QM F5512, left distal fragment, northeastern South Austalia, age uncertain. Although the distal end is solidly fused, the shaft has a surface texture that suggests a juvenile bird.

De Vis did not specify where QM F5512 was found when he named it as a new genus and species of wader, Charadrii (= Limicolae). Without any explanations *Ocyplanus proeses* was included with the gulls, Laridae, by Lambrecht (1933), Brodkorb (1967) and Fisher (1983), and with the rails, Rallidae, by Condon (1975). When compared with QMF 5512 and the tarsometatarsi of waders and flamingoes, those of gulls and rails differ in that from a medial view the medial part of the trochlea for digit II is more rounded.

We agree with de Vis that QM F5512 is similar in size to the tarsometatarsus of a stone-curlew, *Burhinus magnirostris*, but QM F5512 and the tarsometatarsi of flamingoes differ from stone curlews in having a more gradual expansion of the distal end, and also in that the trochlea for digit II does not extend as far distally relative to that

TABLE 12. Measurements in mm of the tibiotarsi and tarsometatarsi of North American Quaternary flamingoes from Shufeldt (1884), Miller (1944), Howard (1955) and Rich and Walker (1983).

	P. minutus n = 1	*P. stocki* n = 1	*P. copei* n = 2
Tibiotarsus			
Width of distal end	12.7	@13	17
Depth of external condyle	@15	*16.2	20
Anterior length of interior condyle		6.2	
Tarsometatarsus			
Width of distal end			20-22
External depth of trochlea II			8.6-9.4
Anterior width of trochlea II			7.6-8.6
Internal depth of trochlea III			10.1-10.6
External depth of trochlea III			10.6-10.7
Anterior width of trochlea III			7.9-9.4
Posterior length of trochlea III			11.3-12.8
Internal depth of trochlea IV			9.4-10.5
Posterior width of trochlea IV			5.2-6.2

* 16.0 in Howard (1955).

for digit III. In these respects QM F5512 and the tarsometatarsi of flamingoes resemble those of some other waders with long, slender legs such as lapwings, *Vanellus*, Charadriidae; avocets and stilts, *Recurvirostra, Himantopus* and *Cladorhynchus*, Recurvirostridae; curlews and godwits, *Numenius* and *Limosa*, Scolopacidae; and pratincoles, *Stiltia*, Glareolidae; but their trochleae for digit II extend even less distally than those in QM F5512 and flamingoes (Fig. 5).

QM F5512, the holotype of *Ocyplanus proeses*, conforms to the diagnosis by Miller (1963) for *Phoeniconaias gracilis* (see below) and is similar in size and shape to the holotype. It differs from the tarsometatarsi of *Phoenicoparrus* and *Phoenicopterus* in being more mediolaterally compressed when viewed distally, thus resembling the tarsometatarsus of the living *Phoeniconaias*.

HOLOTYPE OF *IBIS* (?) *CONDITUS*

Femur: QM F5519, left, Wurdulumankula, South Australia, age uncertain.

De Vis (1905) made this femur the holotype of a new species of ibis, Threskiornithidae (= Ibididae). He compared the femur with that of the Straw-necked Ibis, *Threskiornis* (*Carphibis*) *spinicollis*, and noted that the shaft of QM F5519 was relatively stout compared with the length of the femur. In this respect QM F5519 is similar to the femora of Phoenicopteridae, as it is also in other respects, including the sharply curved line in the popliteal area mentioned by de Vis.

The femur differs from that of all living genera of flamingoes in that the anterior intermuscular line is straight over much of its length except near the proximal end where it is highly concave, curving medially to touch the trochanter; the anterior face of the shaft near the proximal end is deeply excavated and lacks a pneumatic foramen (Lambrecht 1933); the ligamental pit at the base of the fibular condyle, when viewed posteriorly, is relatively deeper, and a distinct ridge lies just proximal to that; proximal to the prominent ridge is a deep channel that runs onto the shaft (modern flamingoes lack the well defined channel, and the ridge is only hinted at).

In size, QM F5519 is smaller than the femora of *Phoeniconaias minor* and is from a bird similar in size to QM F5512; we, therefore, refer QM F5519 to *Ocyplanus proeses*.

HOLOTYPE OF *PHOENICONAIS GRACILIS*

Tarsometatarsus: SAM P13650, left distal fragment, Lake Kanunka, Site 1, UCMP V-5772 South Australia, Tirari Formation, Pliocene.

Miller (1963) described this tarsometatarsus as the holotype of a new species of flamingo with a tarsometatarsus smaller and more slender than that of *Phoeniconaias minor*, the smallest extant species of flamingo. He suggested that the fossil resembled most the African *Phoeniconaias*, because it had a trochlea II that was relatively shallow and less rounded than in other living genera. This seems variable within our samples of living genera. The tarsometatarsus of *Phoeniconaias* is however, like the Australian fossil, more mediolaterally compressed than those in the species of *Phoenicoparrus* and *Phoenicopterus*. *P. gracilis* differs from *Leakeyornis* in that trochlea IV is narrower posteriorly and deeply incised laterally, and in distal view, the tarsometatarsus is more compressed mediolaterally. *Phoeniconotius* has much shallower trochleae relative to their width and a less compressed distal end. We agree with Miller's diagnosis, which equally applies to the holotype of *Ocyplanus proeses*, a name that has priority and to which we refer SAM P13650, the holotype of *Phoeniconaias gracilis*.

ADDITIONAL REFERRED MATERIAL

Tibiotarsus: UCMP 56887, right distal fragment, Lake Kanunka, Site 1, UCMP V-5772, South Australia, Tirari Formation, Pliocene.

Miller (1963) referred this tibiotarsus to *Phoeniconaias gracilis*, because it is smaller than that of *P. minor*, which it resembles in shape. It further differs from all of the extant flamingoes we examined in that: the ligamental groove on the external shaft surface near the distal end lies close to the anterior border of the shaft and does not course diagonally across that surface; and the distal end is not flattened distally, but both internal and external condyles slope proximally and posteriorly, although this is certainly overemphasized by postdepositional wear. It differs from the tibiotarsus of *Xenorhynchopsis tibialis* in flaring more broady distally, in having less prominent ligamental protuberences on the anterior surface, and in having the ligamental groove on the lateral face of the external condyle located more anteriorly. It differs from the tibiotarsus UCMP 60562, that we tentatively refer to *Phoenicopterus ruber*, in having a decidedly deeper tendinal canal on the anterior surface and relatively higher ligamental prominences. It differs from the tibiotarsus of *Xenorhynchopsis minor* in that the condyles, viewed from the side, have a more pronounced slope proximoposteriorly. We refer UCMP 56887 to *Ocyplanus proeses*.

Tarsometatarsus: UCMP 60561, right distal fragment, Lake Kanunka, Stirton Quarry, Site 1, UCMP V-5772 South Australia. Found as float, Pliocene or Quaternary.

Miller (1963) referred this tarsometatarsus to *Phoeniconaias gracilis*. It is slightly smaller than the smallest individual in our *P. minor* sample and poorly preserved. We tentatively refer UCMP 60561 to *Ocyplanus proeses*.

Phoenicopteridae, indet.

Sternum: UCMP 69588, anterior fragment, locality uncertain, South Australia.

Sternum: UCMP 128455, anterior fragment of a juvenile, Manku, Kallakoopah Creek, UCMP V-76056, South Australia, Quaternary.

Both UCMP 69588 and 128455 are fragments of the manubrial end of the sternum. The manubrial spine is preserved complete in 69588. UCMP 128455 appears to be a juvenile, based on the porous appearance of the bone surface and its small size. On the ventral side the angle of lateral spread posteriorly between the coracoidal sulci is greater than in *Phoenicopterus ruber, P. chilensis* and *Phoeniconaias minor*, but the vertical depth of the coracoidal sulci is in the adult UMCP 69588 similar to *P. ruber*, and in the juvenile and worn UCMP 128455 less than in *P. ruber*. These characters might be diagnostic when more complete fossil sterna become available, but at this stage we can assign UCMP 69588 and UCMP 128455 only to indeterminate Phoenicopteridae.

DISCUSSION AND CONCLUSIONS

Modern genera of flamingo differ in the shapes of the mandibles and in the presence (*Phoenicopterus* and *Phoeniconaias*) or absence (*Phoenicoparrus*) of a hind toe (Salvadori 1895). Unfortunately *Phoenicopterus* and *Phoeniconaias* lack a hallux scar on the tarsometatarsus to indicate that they have a hind toe. *Phoeniconotius* is the only genus of flamingo known to have a hallux scar (Miller 1963; Rich and Walker 1983). Lambrecht (1933) noted that *Ocyplanus* did not have a hallux scar.

Brodkorb and Mourer-Chauvire (in press) believe that the post-cranial bones of flamingoes are of limited diagnostic value. As indicated above in the descriptions of the fossils, we, as did de Vis (1905) and Miller (1963), found some differences in shape, that may be generic, but more complete fossil material is needed to substantiate their significance. The only Pliocene and Quaternary material of Australian flamingoes available to de Vis included seven, to Miller six, and to us 18 bones.

The limited evidence available suggests that sometime during this time period there were at least four species of flamingo, in what may be three different genera, and that they were restricted to the Lake Eyre Basin of northeastern South Australia.

The range in size and at certain stratigraphic levels the number of sympatric genera and species of the Pliocene and Quaternary flamingoes of Australia is greater than has been recorded elsewhere in time and space. *Xenorhynchopsis tibialis* appears to have been larger than any known flamingo except for *Phoeniconotius eyrensis* of the Australian Miocene, and *Ocyplanus proeses* appears to have been smaller than any known flamingo except for *Leakeyornis aethiopicus* of the African Miocene. *Xenorhynchopsis minor* appears to have been similar in size to *Phoeniconaias minor*, the Lesser Flamingo, and smallest of the five species of modern flamingoes; whereas *Phoenicopterus ruber*, the Greater Flamingo, is the largest of the modern flamingoes.

Xenorhynchopsis differs from other genera of flamingoes mainly in having a tibiotarsus with a relatively deep distal end, which flares little, especially on the lateral side.

Australian fossil flamingoes assigned to *Phoenicopterus ruber* are the size of this living species, but some elements demonstrate a few differences from this species and other known genera of flamingo. We, therefore, retain some of the Australian fossils in this genus for convenience only. It should be noted however, that we suspect that at least UCMP 60562 from Lake Kanunka may merit description as a new taxon when more diagnostic material is available.

In *Ocyplanus proeses*, we include *Ibis* (?) *conditus* and *Phoeniconaias gracilis*. Although the tarsometatarsi of *O. proeses* are qualitatively indistinguishable from those of *Phoeniconaias minor*, the referred femur and tibiotarsus differ markedly. Thus, because *O. proeses* does not conveniently fit into any known genus of flamingoes we have retained the de Vis name, which has priority.

It has not been feasible to date radiometrically the sites that have yielded flamingo bones, some of which were found as 'float' on erosion surfaces in creek beds. It appears that four species are known from the Cooper Creek localities (Table I), three from Lake Kanunka, and one specimen from Kallakoopa Creek. The Cooper Creek localities may include sites of various ages within the Pleistocene. The six Kanunka fossils, however, probably represent contemporaneous Pliocene forms, suggesting that at least three species inhabited this area, which must have had permanent saline lakes in the Pliocene, and missing *Xenorhynchopsis tibialis* may represent a species restricted to the Pleistocene that frequently crops out along Lower Cooper Creek. The smallest flamingo, *Ocyplanus proeses*, occurs in both places but is restricted to only one Cooper Creek locale, Wurdulumankula, the age of which is uncertain. It has not been found anywhere together with *Xenorhynchopsis tibialis*, and could be restricted to the Pliocene. *X. minor* is long ranged, from Pliocene into the Quartenary.

How the Australian flamingoes are related to those elsewhere in the world cannot be determined until more complete material of fossil forms is available. It does seem clear that there were several kinds of flamingoes in Australia during the Pliocene and Quaternary (Rich and van Tets 1982) and, as happened in North America, increased aridity accompanied by the disappearance of reasonably permanent shallow lakes, and of feeding and breeding grounds, resulted during the Quaternary in major extinctions. In North America flamingoes survived in the Caribbean Basin, whereas the antipodean flamingoes left no survivors, even though Australia had hosted during the last 3-4 million years one of the most, if not the most, diverse flamingo faunas. Better dating of the sites containing flamingoes in Australia could provide significant data for timing of extinctions and reconstruction of changing palaeoenvironments.

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LITERATURE CITED

BLAKE, E.R., 1977. 'Manual of Neotropical Birds'. Vol. 1. (Univ. of Chicago Press: Chicago). 674 pp.

BOWLER, J.M., 1982. Aridity in the late Tertiary and Quaternary of Australia. *In*: 'Evolution of the Flora and Fauna of Arid Australia'. (Eds Barker, W.R. and Greenslade, P.J.M.). pp. 35-45. (Peacock Publ., Frewville: South Australia).

BRODKORB, P., 1967. Catalogue of fossil birds Part 3. *Bull. Florida State Mus.* **11**(3): 99-220.

BRODKORB, P., and MOURER-CHAUVIRE, C. (in press). The fossil flamingoes of Early Man sites of Olduvai Gorge (Tanzania). *Ostrich.*

BROWN, L.H., URBAN, E.K. and NEWMAN, K., 1982. 'The Birds of Africa'. Vol. 1. (Academic Press: London) 521 pp.

CONDON, H.T., 1975. 'Checklist of the Birds of Australia. Pt. 1. Non-passerines'. (Roy. Australasian Ornith. Union: Melbourne) 311 pp.

CRAMP, S. (Ed.), 1977. 'Handbook of the Birds of Europe the Middle East and North Africa'. Vol. 1. (Oxford Univ. Press: Oxford). 722 pp.

DE VIS, C.W., 1905. A contribution to the extinct avifauna of Australia. *Ann. Qd Mus.* 6: 3-25.

FISCHER, K., 1983. Möwenreste (Laridae, Charadriiformes, Aves) aus dem Mitteloligozänen phosphoritknollenhorizont des Weisselsterbeckens bei Leipzig (DDR). *Mitt. zool. Mus. Berlin.* Bd. 59 Suppl.: *Ann. Orn.* 7:151-5.

GREGORY, J.W., 1906. 'The Dead Heart of Australia'. (John Murray: London) 384 pp.

HOWARD, H., 1955. Fossil birds from Manix Lake, California. *Geol. Surv. Prof. Pap.* **264-J**: 199-205.

LAMBRECHT, K., 1933. 'Handbuch der Palaeornithologie'. (Gebrüder Borntraeger: Berlin) 1024 pp.

MILLER, A.H., 1963. The fossil flamingoes of Australia. *Condor.* **65**(4): 289-99.

MILLER, L.H., 1944. A Pliocene flamingo from Mexico. *Wilson Bull.* **56**(2): 77-82.

RICH, P.V., and VAN TETS, G.F., 1982. Fossil birds of Australia and New Guinea: Their biogeographic, phylogenetic, and biostratigraphic input. *In*: 'The Fossil Vertebrate Record of Australasia'. (Eds Rich, P.V. and Thompson, E.M.). pp. 235-384. (Monash Univ. Offset Printing Unit: Clayton).

RICH, P.V. and WALKER, C.A., 1983. A new genus of Miocene flamingo from East Africa. *Ostrich,* **54**: 95-104.

RICH, T.H., ARCHER, M., PLANE, M., FLANNERY, T., PLEDGE, N., HAND, S., and RICH, P., 1982. Australian Tertiary mammal localities. *In*: 'The Fossil Vertebrate Record of Australasia'. (Eds Rich, P.V. and Thompson, E.M.). pp. 525-72. (Monash Univ. Offset Printing Unit: Clayton).

SALVADORI, T., 1895. Catalogue of birds in the British Museum (Natural History) **27**: 8.

SHUFELDT, R.W., 1892. A study of the fossil avifauna of the *Equus* beds of the Oregon Desert. *Journ. Acad. Nat. Sci. Phila.* **9**: 410–411.

STIRTON, R.A., TEDFORD, R.H., and WOODBURNE, M.O., 1968. Australian Tertiary deposits containing terrestrial mammals. *Univ. Calif. Pub. Geol. Sci.* **77**: 1–30.